INSTITUUT VOOR PLANTENZIEKTENKUNDIG ONDERZOEK
WAGENINGEN, NEDERLAND
DIRECTEUR: Dr. J. G. TEN HOUTEN

MEDEDELING No. 258 EN 259

TRANSLOCATION OF LEAF ROLL AND VIRUS Y IN THE POTATO

DOOR

A. B. R. BEEMSTER

EEN VERGELIJKING TUSSEN HET TRANSPORT VAN X-VIRUS EN TWEE VERSCHILLENDE STAMMEN VAN Y-VIRUS IN AARDAPPELPLANTEN

(A COMPARISON BETWEEN THE TRANSLOCATION OF VIRUS X AND TWO DIFFERENT STRAINS OF VIRUS Y IN THE POTATO PLANT)

DOOR

A. B. R. BEEMSTER

OVERDRUK UIT:
PROC. 4th CONF. POTATO VIRUS DIS. BRAUNSCHWEIG, 1960: 60-67, 1961
EN T.PL.-ZIEKTEN, 67: 278-279, 1961

...WEALTH MYCOLO...
18 DEC 1961

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TRANSLOCATION OF LEAF ROLL AND VIRUS Y IN THE POTATO

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INTRODUCTION

Many of the problems concerning seed potato growing are closely connected with questions relating to virus translocation in the potato plant. An exact knowledge on the rate of virus translocation is of interest not only with respect to the date of harvesting, but also many other problems. E.g. the possibility of diagnosing virus in the leaves or tubers of primarily infected plants. Methods of diagnosis can only be applied successfully when we are well informed about the sensitivity of a given moment in relation to the amount of virus present at a given test after the virus has penetrated the part of the plant which is being tested. Besides the fact that a certain concentration of a virus must be present there, we have to keep in mind that certain parts of a plant may be infected and others not, since it has been shown in earlier work (BEEMSTER, 1958b) that the amount of virus that is translocated to a certain part of a plant may be very small and even that there may be virus translocated to one part of the plant (e.g. the tubers) and not to other parts (e.g. the top). In the following, some experiments on the translocation of potato virus Y and leaf roll in the potato will be described.

1. EXPERIMENTS WITH LEAF ROLL VIRUS

a. Experiment in 1957.

On each of the following dates: 29th of May, 5th, 12th and 19th of June, 20 Bintje potatoes were planted in pots. The plants were grown in insect-proof glasshouses at temperatures of 20–24°C. under natural light conditions. The plants were single-stemmed. On the 26th of July when the plants of the different groups were 31, 44, 51 and 58 days old respectively, 10–12 *Myzus persicae*, which had been reared on leaf roll infected potato plants, were put on to the tops of each plant, which were then enclosed in a cellophane bag. The aphids remained on the plants for three days after which they were killed with an insecticide (Lirohex) by spraying the plants. On the 5th, 12th, 19th and 26th of August (10, 17, 24 and 31 days after infection respectively) the tubers of five plants of each group were harvested. In order to obtain data as to whether or not the virus had been translocated downwards to the tubers, the part with the main sprout of each tuber was planted in a pot in the spring of 1958; 6–8 weeks after planting symptoms of leaf roll were visible on the plants. The results of this experiment are given in the first part of table 1. Before discussing these results we will first describe a similar experiment which was performed in 1959.

b. Experiment in 1959.

On the 9th of April, 1959, 75 Bintje potatoes were planted in pots and were grown under the same conditions as the plants used in the 1957 experiment. On the 14th,

[1] The author is greatly indebted to Mr. M. M. MARTIN for correcting the English of the text.

Reprinted from: Proc. 4 th. Conf. Potato Virus Dis. Braunschweig 1960, pp 60-67

21st and 28th of May and on the 4th of June, 35 *Myzus persicae*, which had been reared on leaf roll infected potato plants were put on to the tops of their respective test plants; the first 3 groups comprised 20 plants and the last group 15. The aphids were allowed to feed on the plants for 2 days after which they were killed by spraying the plants with an insectide (Lirohex). Five plants of each group were harvested respectively 6, 12, 18 and 23 days after putting the aphids on to the plants. In the spring of 1960 the part with the main sprout of each tuber was planted in a pot in order that readings could be made as to whether or not the tuber had become infected. The results of this part of the experiment are given in the second part of table 1.

On the same day that the tubers were harvested, the stems of the plants were cut into a number of pieces, each consisting of two nodes. These stem pieces were rooted in soil in order to give the virus, if present in a certain piece, the opportunity to multiply. At the end of the growing period of these cuttings, the tubers produced in the pots were harvested and they in turn were tested in the spring of 1960. By this procedure it was possible to obtain a picture of potato leaf roll virus translocation within the stems of potato plants. The results which were obtained when all tubers had been tested are given in fig. 1.

When we compare the results of the 2 experiments given in table 1 we see that in the first experiment some virus was already translocated 10 days after inoculating in the 2 youngest groups of plants, whereas in the second experiment this was the case as early as 6 days after inoculation.

TABLE 1. The percentage of infected tubers of Bintje potatoes at different intervals after inoculation when inoculated at different intervals after planting.

Experiment in 1957

Date of planting	Date of inocu-lation	Age in days	Days after inoculation			
			10	17	24	31
19 June	26 July	37	4/14[1] = 29%	14/34 = 41%	18/41 = 44%	10/32 = 31%
12 June	26 July	44	1/32 = 3%	6/27 = 22%	6/43 = 14%	11/37 = 30%
5 June	26 July	51	0/32 = 0%	3/32 = 9%	11/37 = 30%	13/38 = 34%
29 May	26 July	58	0/32 = 0%	1/51 = 2%	0/44 = 0%	2/40 = 5%
Experiment in 1959			6	12	18	23
9 April	14 May	35	no tubers	6/6 = 100%	34/34 = 100%	37/37 = 100%
9 April	21 May	42	no tubers	22/23 = 96%	24/30 = 80%	30/30 = 100%
9 April	28 May	49	3/28 = 11%	19/31 = 61%	24/30 = 80%	25/30 = 83%
9 April	4 June	56	–	12/30 = 40%	15/30 = 50%	12/30 = 40%

[1] numerator/denominator = number of infected tubers/total number of tested tubers.

The results of both experiments show clearly that the older the plants are at the moment of inoculation, the less virus is translocated downwards to the tubers. This phenomenon, called mature plant resistance, was already detected in earlier experiments on leaf roll and virus X (BEEMSTER, 1954, 1958a, b).

It is remarkable that in 1959 the rate of infection of tubers was much higher than in 1957. Possibly this has to be attributed to the fact that in 1959 the number of viruliferous aphids put on to each plant was much higher than in 1957, viz. in 1957 10–12

aphids per plant and in 1959, 35 aphids per plant. Whether environmental conditions such as light intensity and day length also played a role is not known. From experiments with leaf roll virus over a number of years we know that the rate of infection obtained in such experiments is very variable. A second fact that can be noted is that the rate of tuber infection found at about 2 weeks after inoculation did not differ from that found in the groups which were harvested at a later date. Apparently little virus is translocated to the tubers after a certain level of tuber infection is reached. This level greatly depends on the age of the plants at the time of inoculation.

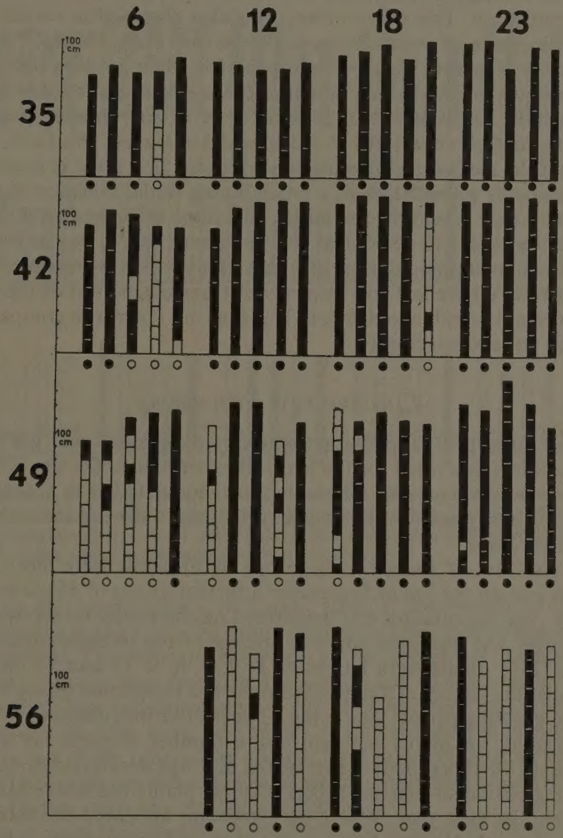

FIG. 1. Translocation of potato leaf roll virus through the stems of potato plants after placing viruliferous aphids on the tops. The plants were infected 35, 42, 49 and 56 days after planting, respectively, and were investigated in units of 5 plants 6, 12, 18 and 23 days after inoculation respectively. Where a part of the stem proved to be healthy this is shown in white; where it proved to be infected, in black. Whether or not one or more infected tubers were found is indicated by white or black circles at the foot of each plant.

The translocation of leaf roll virus through the stems of the plants is given schematically in fig. 1. It is clear that once the leaf roll virus starts moving it reaches the tubers rather quickly. There were few cases in which translocation of virus was found without associated infection of the tubers of the plant (plant 5 in the first group; 3, 5 and 15 in the second group; 2, 3, 4, 9 and 11 in the third group and none in the last group). This was generally only found shortly after infection. In some of the plants it was found that the virus had apparently passed a certain part of the stem without remaining there or that at least the virus could not be detected there by the method that was used. This suggests that during the first stages of virus translocation the virus moves only in very small concentration. This phenomenon was also observed in earlier experiments concerning translocation of potato virus X (BEEMSTER, 1954, 1958b).

In the last group of plants which were inoculated when 56 days old, a number of plants did not become infected at all. Apparently the plants had by then become more resistant to infection. In experiments with virus X it was always possible, even in rather old plants, to detect the virus in the inoculated leaves. We have, however, to keep in mind that the mechanical inoculation with sap, as is done in experiments with virus X, most probably gives the plant a much higher initial infection than is the case with leaf roll when only relatively few initial infections are introduced by the aphids. Moreover it is not possible to detect leaf roll virus in as easy a way as is the case with virus X, since mechanical inoculation of a test plant which is possible for X, is not possible for leaf roll. Where leaf roll virus is not translocated out of the leaves to the stem it is therefore not possible to detect it. It is thus not correct to compare the results with leaf roll and virus X too closely.

2. EXPERIMENTS WITH VIRUS Y

On the 10th of July, 1957, 155 Bintje potatoes were planted and grown under the greenhouse conditions described for the leaf roll experiments. On the 17th of August, when the plants were 38 days old, 60 plants were inoculated with a normal strain of virus Y. Thirty of these plants were inoculated on one of the top leaves and 30 plants on one of the lower leaves.

On the 24th and 31st of August, two groups of 30 plants were inoculated on one of the top leaves and on the 7th of September a further group of 35 plants was treated in the same way. The inoculation was performed mechanically by sap with carborundum as an abrasive. The infectious sap was obtained from recently-infected *Nicotiana glutinosa* plants. Five plants were harvested at 2, 4, 6, 9, 11 and 13 days after each inoculation, whilst the last set of 5 plants from the last inoculated group was harvested at the end of the growing period, this being 32 days after inoculation.

The stems from all the plants were cut into a number of parts, as was described before for the leaf roll experiment. Most of the cuttings developed symptoms during their first growing period so that the tubers of these plants did not require harvesting for further testing the next year. Where no symptoms appeared the tubers were harvested and tested the next year. It appeared that making cuttings from rather old potatoes leads to a great number of failures. We are therefore not able to give results on translocation through the stem of the last part of the third, and of the fourth group. The results of the experiment are given in fig 2 in the same way as was done for the leaf roll virus.

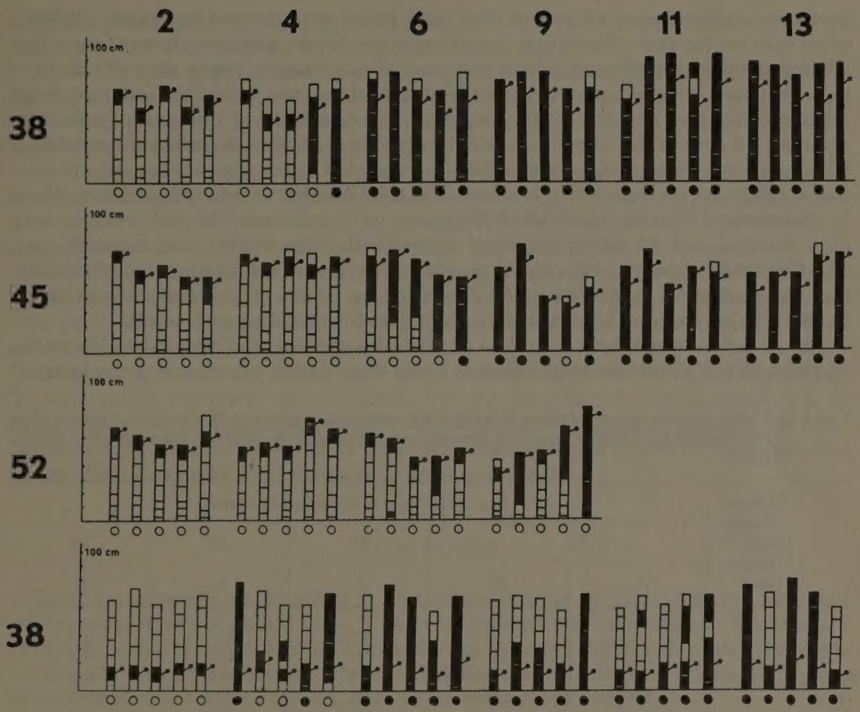

FIG. 2. Translocation of potato virus Y through the stems of potato plants after mechanical inoculation. Inoculations were made 38, 45, 52 and 59 days after planting. Five plants at a time were investigated 2, 4, 6, 9, 11 and 13 days after inoculation respectively. The position of the leaf which was inoculated is indicated by a black circle.

Fig. 2 shows that translocation of potato virus Y downwards to the tubers could already be detected in the youngest group four days after inoculation of either the top leaf or an older leaf. The older the plants are at the moment of inoculation, the longer it takes for the virus to pass from the inoculated leaf to the tubers. Here again it is clear that mature plant resistance plays a role. Furthermore fig. 2 shows that there is a strong tendency that the virus first moves downwards and later upwards. This implies that infection of the tubers may already have taken place long before symptoms are visible in the plant. On the other hand we can state that whenever symptoms are visible in the plants, virus has reached the tubers.

The picture of virus translocation upwards in the stem from one of the lower leaves shows some irregularities. Sometimes the virus was only translocated downwards and sometimes both up- and downwards. It is possible that had we inoculated somewhat earlier, upward movement would have taken place in all plants and that had we inoculated some days later only downward translocation would have occurred.

The tubers of the plants were tested in 1958 for the presence of virus Y. In this ex-

periment all the eyes of all tubers from each plant were planted separately. Table 2 gives data on the rate of infection found in plants, tubers and eyes. It was found that when a plant yields infected tubers this does not necessarily imply that all tubers of that plant are infected; moreover not all the parts of one tuber are infected in all instances. To give an idea of the frequency of occurrence of this partial infection, summarized data of this experiment will be given here. As can be derived from table 2, 52 plants were found to produce at least one infected tuber. From these only 14 produced tubers which were 100% infected. The total number of tubers tested from these 52 plants was 352, from which 195 (56%) were 100% infected; 120 (34%) tubers were quite healthy and 37 (10%) produced tubers with both healthy and infected eyes. The frequency of partial infection depends on the time of inoculation and of harvesting. The number of tubers harvested in each group of this experiment was too small to give reliable data, we have therefore given data for the group as a whole.

The 37 tubers which were found to be partially infected were divided in 183 parts, of which 77 (42%) proved to be infected. From these data it becomes clear that partial

TABLE 2. Translocation of potato virus Y from the leaves to the tubers in Bintje potato plants after inoculation in different stages of growth and harvesting at different intervals after inoculation.

	Number of days after inoculation	Age at the time of inoculation (days)				
		38		45	52	59
		A[1]	B	A	A	A
Infection per plant	2	–	–	0/5	0/5	0/5
	4	–	–	0/5	0/5	0/5
	6	–	–	1/5	0/5	0/5
	9	5/5[2]	5/5	4/5	0/5	0/5
	11	5/5	5/5	5/5	0/5	0/5
	13	5/5	5/5	5/5	0/5	2/5
	32	–	–	–	–	5/5
Infection per tuber	2	–	–	0/27 = 0%	0/37 = 0%	0/24 = 0%
	4	–	–	0/22 = 0%	0/27 = 0%	0/29 = 0%
	6	–	–	1/27 = 4%	0/36 = 0%	0/25 = 0%
	9	31/36[3] = 86%	23/26 = 89%	9/33 = 27%	0/27 = 0%	0/22 = 0%
	11	38/43 = 88%	21/36 = 58%	16/30 = 53%	0/27 = 0%	0/26 = 0%
	13	32/40 = 80%	28/32 = 88%	11/32 = 34%	0/27 = 0%	4/25 = 16%
	32	–	–	–	–	19/32 = 59%
Infection per eye	2	–	–	0/71 = 0%	0/86 = 0%	0/129 = 0%
	4	–	–	0/54 = 0%	0/128 = 0%	0/138 = 0%
	6	–	–	1/88 = 1%	0/157 = 0%	0/129 = 0%
	9	57/71[4] = 80%	54/58 = 93%	19/103 = 18%	0/148 = 0%	0/115 = 0%
	11	83/95 = 87%	85/117 = 73%	35/107 = 33%	0/159 = 0%	0/100 = 0%
	13	109/137 = 80%	81/87 = 93%	49/139 = 35%	0/158 = 0%	13/107 = 12%
	32	–	–	–	–	65/136 = 48%

[1] A: One of the top leaves inoculated.
B: One of the lower leaves inoculated.
[2] Numerator/denominator: number of plants with one or more infected tubers/number of test plants.
[3] Numerator/denominator: number of infected tubers/number of tested tubers.
[4] Numerator/denominator: number of infected eyes/number of tested eyes.

infection indeed may be of some importance and may lead to some failures when we want to test potato tubers by indexing only one eye per tuber.

From the data given in table 2 it follows that there is no difference in the rate of infection when a top leaf or one of the lower leaves is inoculated. Differences may exist when the plants are older at the time of inoculation, as was found in earlier experiments with virus X (BEEMSTER, 1954).

Mature plant resistance was detected to a high degree and apparently somewhat stronger than in the case of leaf roll, when we compare the data from the tables 1 and 2. A curious fact was found in the last group of plants. It can be seen that already 13 days after inoculation more infection of tubers was detected than in the group that was inoculated one week earlier. It is not quite clear what is the cause of this. Possibly a period of resistance is followed by a period in which again a quicker translocation can take place. However, this is the only experiment in which we found this, so possible environmental conditions have played a role.

Concluding, we can say that mature plant resistance both to leaf roll and a normal Y strain could be clearly demonstrated. For the growing of seed potatoes it is of importance to know this as all measures such as pre-sprouting, early planting, etc must be considered as very important as they favor a quick development of the plants and brings them to a more resistant stage as soon as possible.

SUMMARY

Some experiments are described in which translocation of potato leaf roll virus and of a normal strain of potato virus Y in potato plants was investigated. The translocation of both leaf roll and virus Y proved to be the more difficult the older the plants were at the time of inoculation. There is evidence that mature plant resistance is more pronounced in the case of virus Y than in the case of leaf roll.

From data on the occurrence of partial infection of virus Y in the tubers it appeared that primarily infected plants regularly produce both healthy and infected tubers. From plants that produced at least one infected tuber 37 out 352 tubers were found to be partially infected.

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DISCUSSION

THUNG: In China the differences between day and night temperatures of the soil, called thermal periodicity, are claimed to be of paramount importance for the physiology of plants. Does Dr. BEEMSTER have any experience regarding plants with several differences of day and night temperatures e.g. in greenhouses and outdoors?

BEEMSTER: Regarding potato virus X we obtained quite the same results both in greenhouse experiments and in the field. Concerning virus Y or leaf roll virus it is very difficult to do field experiments as it is not possible to settle the exact time of infection, caused by naturally occurring aphids.

ROSS: The results of Dr. BEEMSTER show that in the variety Bintje potato virus Y migrates remarkable faster than leaf roll virus. These differences depend on the variety used. We know varieties which propagate virus Y much more slower than leaf roll virus. In varieties most resistant against virus Y lower percentages of the tubers are infected than are the percentages of leaf roll-infected tubers of those varieties known as the most leaf roll resistant ones.

HARRISON: To what extent can the transport of viruses into the stems and tubers of potato plants be correlated with the number of initial infections per plant?

BEEMSTER: Regarding potato viruses X and Y we have evidence of a correlation between number of initial infections per plant (per leaf) and total amount of virus that is translocated downwards to the tubers. It is rather difficult to study this problem as a rather low concentration of virus in the inoculum may cause an optimal effect on the rate of tuber infection under the prevailing conditions. Therefore, correlations can be found only if we are working with low virus concentrations in the inoculum. The time at which some virus reaches a tuber is hardly affected by differences in the number of initial infections, viz. only in so far chance has some influence.

KORTE MEDEDELING

T. Pl.-ziekten 67 (1961): 278–279

EEN VERGELIJKING TUSSEN HET TRANSPORT VAN X-VIRUS EN TWEE VERSCHILLENDE STAMMEN VAN Y-VIRUS IN AARDAPPELPLANTEN[1]

With a summary: A comparison between the translocation of virus X and two different strains of virus Y in potato plants

DOOR

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Het optreden van een voor Nederland nieuwe stam van het aardappel-Y-virus, in Duitsland bekend onder de naam „Tabak-Rippenbräune-Virus", gaf aanleiding tot de vraag, in hoeverre het transport van dit virus van het blad naar de knollen in de aardappelplant overeenkomst vertoont met het gewone Y- en het X-virus. Daarom is hierover in 1960 een proef uitgevoerd, waarbij aardappelplanten van het ras Bintje in drie verschillende stadia van ontwikkeling (respectievelijk 7, 9 en 11 weken na het poten) door middel van sap op een der bladeren met de desbetreffende virussen werden geïnoculeerd. Dit sap was afkomstig van aardappelplanten van de rassen Bevelander, Paul Krüger en Record voor respectievelijk X-virus, de gewone en de nieuwe stam van Y-virus. In navolging van DE BOKX (1961) zal bij de verdere bespreking van de proef de gewone stam van Y-virus met Y en de nieuwe stam met Y^N worden aangeduid.

De proef werd uitgevoerd in een luisvrije kas. Van de op de drie genoemde tijdstippen geïnoculeerde planten werden respectievelijk 10, 17 en 24 dagen na inoculatie 8 planten gerooid. Eind 1960 en begin 1961 werden de knollen van de planten gepoot om na te gaan in hoeverre hierin virus aanwezig was. De toetsing van de planten op de aanwezigheid van X-virus geschiedde met de toetsplant *Gomphrena globosa*, terwijl de aanwezigheid van de beide Y-virusstammen door visuele beoordeling werd vastgesteld. Bovendien werden alle uiterlijk gezonde planten van het gedeelte der proef betreffende het Y^N-virus nog met de toetsplant A6 onderzocht. Hieruit bleek, dat toch een klein aantal van deze planten besmet was.

In tabel 1 zijn de resultaten van de toetsingen per groep van 8 planten samengevat. We zien, dat in de proef met X- en Y-virus de ouderdomsresistentie, zoals deze in vroeger uitgevoerde proeven kon worden aangetoond (BEEMSTER, 1958, 1961) normaal tot uiting komt. Het gedeelte der proef betreffende het Y^N-virus toont daarentegen duidelijk aan, dat van ouderdomsresistentie nagenoeg niet kan worden gesproken. Het transport van dit virus blijkt nl. zowel in de jonge als in de oudere planten zeer snel te hebben plaats gevonden, zoals o.a. duidelijk blijkt uit de gegevens over de besmetting 10 dagen na inoculatie.

Maatregelen, die er op gericht zijn om bij de teelt van pootaardappelen gebruik te maken van de ouderdomsresistentie, zullen dus ten aanzien van het

[1] Aangenomen voor publikatie 29 mei 1961.

TABEL 1. De mate van besmetting van aardappelknollen met X-virus en twee verschillende stammen van Y-virus in samenhang met het tijdstip van inoculatie en het tijdsverloop tussen infectie van het loof en infectie van de knollen.
Rate of infection of potato tubers with virus X and two different strains of virus Y in relation to the time of infection of the plants and the period between inoculation and harvest.

Virus *Virus*	Leeftijd op tijdstip van inoculatie (weken) *Age at the time of inoculation (weeks)*	Aantal dagen na inoculatie *Number of days after inoculation*		
		10	17	24
X	7	11/30 = 37 %	28/35 = 62 %	70/77 = 91 %
	9	0/66 = 0 %	3/65 = 5 %	17/76 = 22 %
	11	3/65 = 5 %	7/54 = 13 %	0/56 = 0 %
	7	7/35 = 20 %	21/40 = 53 %	51/72 = 71 %
Y	9	9/54 = 17 %	30/51 = 59 %	43/54 = 80 %
	11	0/47 = 0 %	8/57 = 14 %	20/48 = 42 %
	7	23/27 = 85 %	33/33 = 100 %	52/53 = 98 %
Y^N	9	43/44 = 98 %	53/55 = 96 %	59/59 = 100 %
	11	39/42 = 93 %	63/72 = 88 %	51/52 = 98 %

[1] Teller/noemer: aantal geïnfecteerde knollen/aantal getoetste knollen
Numerator/denominator: number of infected tubers/number of tested tubers

Y^N-virus bij het ras Bintje stellig tot een geringer resultaat leiden dan ten aanzien van andere op dit punt onderzochte aardappelvirussen.

Bij de uitvoering van bovenbeschreven proef werden over een aantal andere aspecten van het virustransport eveneens gegevens verkregen. Hierover zal in een uitvoeriger publikatie mededeling worden gedaan.

SUMMARY

The translocation of virus X and two strains of virus Y, viz. a normal strain (Y) and the tobacco veinal necrosis strain (Y^N) was studied. It was again evident that Bintje potato plants showed normal mature plant resistance to the viruses X and Y as was found in earlier experiments (BEEMSTER, 1958, 1961). However, translocation of Y^N was much quicker than of the two fore-mentioned viruses; this was found to be even so in the case of rather old plants. Mature plant resistance to Y^N could not be demonstrated distinctly. This fact must be of importance in the epidemiology of this strain of virus Y.

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